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Faunal changes and geographic crypticism indicate the occurrence of a biogeographic transition zone along the southern East Pacific Rise

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ABSTRACT

Aim Deep-sea hydrothermal vents have now been reported along all active mid-ocean ridges and back-arc basins, but the boundaries of biogeographic entities remain questionable owing to methodological issues. Here we examine biogeographic patterns of the vent fauna along the East Pacific Rise (EPR) and determine the relative roles of regional and local factors on the distribution of biodiversity associated with mussel beds along a poorly explored zone, the southern EPR (SEPR).

Location East Pacific Rise.

Methods A species list of macrobenthic invertebrates along the EPR was compiled from the literature and supplemented with data recovered during the French research cruise BIOSPEEDO carried out in 2004 along the SEPR. Biogeographic patterns were assessed by combining the identification of morphological species with a molecular barcoding approach. A multivariate regression tree (MRT) analysis was performed to identify any geographic breaks, and an empirical distribution of species richness was compared with predictions provided by a mid-domain effect model. Macrofaunal community structure associated with mussel beds along the SEPR was analysed in relation to environmental factors using cluster and canonical redundancy analyses.

Results Sequencing of the cytochrome *c* oxidase subunit I gene revealed the occurrence of several cryptic species complexes along the EPR, with the equator separating the southern and northern clades. Furthermore, during the BIOSPEEDO cruise at least 10 still unnamed species were collected between 7°25' S and 21°33' S. The shift in community structure identified by MRT analysis was located south of 17°34' S or south of 13°59' S, depending on the data used, suggesting that the southern part of the SEPR (17°25'–21°33' S) constitutes a biogeographic transition zone in the vent fauna along the EPR. At a regional scale, latitude combined with the type of venting was significantly correlated with the community structure associated with mussel beds.

Main conclusions Together, the molecular data, *in situ* observations, and the distribution of species suggest that the high diversity of vent fauna species presently observed between 17°25' S and 21°33' S is probably a result of the overlap of several distinct biogeographic provinces. We argue that this area thus constitutes a biogeographic vent fauna transition zone along the EPR.

Keywords

Biogeographic patterns, community structure, East Pacific Rise, hydrothermal vents, marine biodiversity, molecular systematics, mussel beds, species richness.

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INTRODUCTION

The discovery of dense communities of endemic species associated with hydrothermal vents on the Galapagos Rift in 1977 offered a new perception of deep-sea benthic fauna, far different from that commonly accepted for the vast and unproductive abyssal plain (Lonsdale, 1977). Hydrothermal vents represent discontinuously distributed oases along oceanic ridges and back-arc basins, volcanic arcs and active seamounts. They are characterized by an ephemeral vent-fauna life span related to tectonic events and/or volcanic activity. The associated marine communities harbour high densities of macrobenthic fauna and have low species richness and low diversity, resulting from the overwhelming numerical dominance of a few species. Organisms are clustered around vents, where they thrive on microbial chemoautotrophic primary production (Van Dover, 2000). These oases are characterized by variable numbers of rare species that are heterogeneously distributed in time and space, depending on the vent conditions and the faunal succession occurring during the early colonization of new vent emissions (Jollivet, 1996; Shank *et al.*, 1998). In the Pacific Ocean, the vent fauna has adapted to the marked instability of the habitat, as strong variations in the geological setting (in relation to magmatic and/or tectonic activity) and the physico-chemical conditions (related to the temporal dynamics of the fluid discharge) naturally occur on a broad range of spatial (centimetres to thousands of kilometres) and temporal (seconds to years) scales (Juniper & Tunnicliffe, 1997; Sarrazin *et al.*, 1997).

Endemism at the specific and generic levels has raised questions about the origin and evolution of vent species: it has been suggested that important groups of vent invertebrates originated and then independently evolved from the late Cretaceous and early Tertiary, that is, from around 65 Ma (Little & Vrijenhoek, 2003). However, the colonization pathways and the links between hydrothermal systems in the global ocean are still poorly understood, despite the growing literature addressing biogeographic questions that has emerged during the last decade (e.g. Tunnicliffe & Fowler, 1996; Tunnicliffe *et al.*, 1998; Van Dover *et al.*, 2002; Tyler *et al.*, 2003; Desbruyères *et al.*, 2006a; Bachraty *et al.*, 2009). The present distribution of vent fauna mainly reflects historical events (i.e. plate tectonics) and the abilities of species to colonize distant territories (i.e. dispersion and migration) (see review in Tunnicliffe *et al.*, 1998). While dispersal and migration are major processes linking neighbouring vent communities (Tunnicliffe & Fowler, 1996), the distance between neighbouring vents and habitat availability depends on the geodynamic nature of the ridge (i.e. volcanism or tectonism).

Based on faunal composition, the global ocean ridge system, consisting of a nearly continuous volcanic chain c. 60,000 km long and back-arc spreading centres, is assumed to harbour five main biogeographic provinces, named for the hydrothermal vent fields explored to date: the Northeast Pacific, the East

Pacific Rise (EPR), the West Pacific back-arc basins, the Mid-Atlantic Ridge (MAR), and the Southwest Pacific and Indian Ocean. However, depending on the authors, five to seven biogeographic entities can be erected based on the literature, often differing in delimitations within an ocean (Tunnicliffe, 1991; Tunnicliffe *et al.*, 1998; Van Dover *et al.*, 2002; Tyler *et al.*, 2003; Bachraty *et al.*, 2009). As an example, while the Mid-Atlantic ridge is considered to form a single biogeographic province by most authors (e.g. Tunnicliffe *et al.*, 1998; Tyler *et al.*, 2003; Desbruyères *et al.*, 2006a; Bachraty *et al.*, 2009), Van Dover *et al.* (2002) defined the Azores plateau and the MAR as two distinct provinces. Similarly, depending on the authors, the West Pacific back-arc basins form one or two (north versus south) biogeographic provinces (e.g. Tyler *et al.*, 2003; Bachraty *et al.*, 2009). The differences among authors depend on the methodology and criteria used to define the biogeographic units, as, unlike the case for the coastal ocean, no clear comprehensive classification exists for the deep sea (Spalding *et al.*, 2007). On the other hand, the global species inventory is far from being complete and is still growing with the exploration of new fields.

Since 1977, taxonomists have described 592 morphological species belonging to 320 genera from vents, including 470 species and 251 genera of macrobenthic invertebrates (Desbruyères *et al.*, 2006b; Bachraty *et al.*, 2009). However, not all known vent sites have undergone the same sampling effort, and biodiversity is probably underestimated in poorly explored zones. Moreover, previous biogeographic analyses did not account for the occurrence of sibling species, which are widespread in the marine environment (Knowlton, 1993). In addition to aiding in the identification of morphospecies, molecular systematics is a powerful tool to address biogeographic issues, as it shows how species separate or expand in time and space (Vrijenhoek, 2009). Comparative phylogeography (i.e. the comparison of phylogeographic patterns among multiple co-distributed taxa) has a strong parallel with historical biogeography and can help in the identification of vicariant events unveiled by taxonomy (Arbogast & Kenagy, 2001). To date, cryptic species have been reported from hydrothermal vents for many taxa separated by physical geological discontinuities that offset the ridge system (e.g. Won *et al.*, 2003; Hurtado *et al.*, 2004; Young *et al.*, 2008). Along the EPR, the presence of cryptic species complexes has been highlighted for lepetodrilid species (Johnson *et al.*, 2008; Matabos *et al.*, 2008a). A strong genetic divergence between a northern and a southern lineage was also observed from a set of taxonomic groups, suggesting the occurrence of permeable genetic boundaries around the equator (e.g. Hurtado *et al.*, 2002, 2004; Won *et al.*, 2003; Matabos *et al.*, 2008a). This hypothesis was recently supported by Plouviez *et al.* (2009), who demonstrated that the recent ridge history of the East Pacific Rise led to a vicariant event that induced genetic divergence across the equator about 1.3 Ma for nearly all vent taxa.

The southern East Pacific Rise (SEPR), which is among the fastest spreading ridge centres in the world (150 mm year⁻¹),

is characterized by a high instability in hydrothermal venting often associated with recent effusive volcanism (Auzende *et al.*, 1994; Fouquet *et al.*, 1994; Embley *et al.*, 1998). While this portion of the EPR has been extensively studied from geological, tectonic and geochemical points of view (Auzende *et al.*, 1994; Fouquet *et al.*, 1994; Fornari & Embley, 1995; Fujioka *et al.*, 1995; Embley *et al.*, 1998), few papers have dealt with faunal composition across vent fields and those that have were based on low numbers of sampling units and study sites. The first analyses of faunal assemblages along the SEPR described a fauna similar to that in the northern part of the EPR (Auzende *et al.*, 1994; Geistdoerfer *et al.*, 1995; Halanych *et al.*, 1999). From quantitative sampling units, Van Dover (2002, 2003) proposed that the EPR represents a single hydrothermal biogeographic province over at least 31 degrees of latitude, the differences in faunal composition being attributable solely to the relative abundances of the dominant species and the distribution of rare species. This author suggested that fields are not distant enough to prevent larval and/or adult dispersal in a stepping-stone manner (Van Dover, 2002). However, these conclusions were drawn after the analysis of a single particular habitat, the mussel beds. Recently, based on the presence-absence of species for all hydrothermal vent fields in the global ocean, Desbruyères *et al.* (2006a) and then Bachraty *et al.* (2009) argued that the northern EPR (NEPR) and SEPR are distinct provinces located on opposite sides of the equator. Despite a more or less continuous distribution of the vent fauna along the SEPR, the faunal assemblages consist of a succession of small patches dominated by either vestimentiferan tubeworms, bivalves or stalked cirripeds, each of them resembling assemblages typical of 13° N/9°50' N/EPR for tubeworms, 21° N/EPR for bivalves, or the West Pacific back-arc basins for cirripeds (Jollivet *et al.*, 2005). These observations led to the hypothesis that this ridge portion may represent a transition zone between the NEPR fauna and those of the Atlantic or the West Pacific back-arc basins, where species may have reached their range limits. In this context, the objective of the present study was twofold, as follows.

1. To test the hypothesis that the SEPR could represent a transition zone between the NEPR and the other biogeographic regions found in the Pacific Antarctic Ridge and the Western Pacific. For this, the macrofaunal community structure was compared at two spatial scales: (i) along the whole EPR from 21° N to 21°33' S, using species lists, and then (ii) along the 7°25' S–21°33' S/SEPR portion, using a semi-quantitative dataset from nine mussel beds at six hydrothermal vent fields in order to determine the relative roles of local and regional factors on mussel bed diversity.

2. To generalize the hypothesis of vicariance across the equator over nearly all vent habitats. This was assessed by a barcode analysis of the main gastropod species encountered along the EPR. Gastropod species are indeed an important component of the hydrothermal fauna diversity; they display various life history strategies and are found in all kinds of habitats (Jollivet, 1996; Mills *et al.*, 2007).

MATERIALS AND METHODS

Taxa, regions and data sources

The BIOSPEEDO cruise

The oceanographic cruise BIOSPEEDO, conducted in the south-east Pacific in April/May 2004, aimed to increase our understanding of biodiversity patterns and the processes governing them along the SEPR, a poorly explored but important ridge crossroads between biogeographic vent provinces (Jollivet *et al.*, 2005). Six hydrothermal vent fields, governed by either effusive volcanism or tectonism, were thus intensively surveyed between 7°25' S and 21°33' S (Fig. 1). Areas driven by volcanic activity consist of a dome-shaped ridge crest where hydrothermal conduits resulting from seawater warming are short, shallow and unstable. By contrast, tectonic areas are characterized by a deep axial graben where hydrothermal fluxes are controlled by faults and are more stable through time (Fouquet *et al.*, 1994). This fine-tuned latitudinal survey led to the collection of a large set of biological samples from a variety of habitats (i.e. diffuse venting zones, extinct chimneys, black smokers) and was performed in diverse faunal assemblages dominated by either bivalves, vestimentiferan tubeworms, alvinellids or *Chorocaris* shrimp swarms at 21°33' S. In addition, an important sampling effort on mussel beds was undertaken. A total of

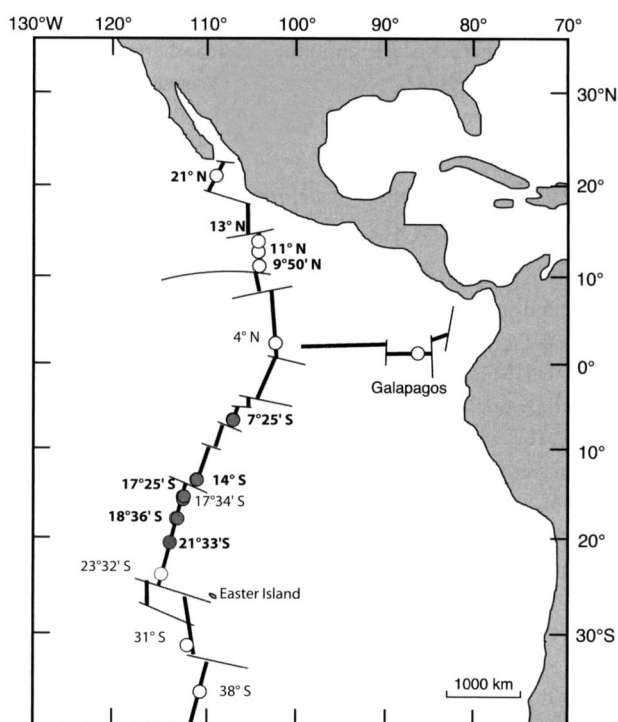


Figure 1 Locations of the hydrothermal vent fields along the East Pacific Rise. Vent fields visited during the BIOSPEEDO cruise along the southern East Pacific Rise are represented in grey. Vent fields included in the global analysis of the macrobenthic invertebrate species list are indicated in bold.

nine semi-quantitative sampling units of *Bathymodiolus thermophilus* beds were collected at six vent fields from both volcanic-dominated and tectonic-dominated zones between 7°25' S and 21°33' S (Table 1). Distances between neighbouring sites ranged from 3 to 891 km, and distance between chimneys within a site (i.e. Grommit) from 30 to 147 m. The study sites appeared to be at different successional stages (following Shank *et al.*, 1998), such that three main types of habitats were sampled: extinct zones, defined as areas with a lack of venting and almost devoid of fauna (moribund sites); diffusing venting areas (diffusion zones); and active black smokers (chimneys). For a brief description of all vent fields, see Jollivet *et al.* (2005).

Benthic communities along the EPR (i.e. the global scale)

A global species list of benthic macrofauna, including only the main invertebrate taxa (i.e. gastropods, polychaetes and echinoderms), was assembled from the data compiled by Desbruyères *et al.* (2006b), and completed with the species list from the BIOSPEEDO cruise. Highly mobile epifauna (e.g. crustaceans) have intentionally been excluded, as they were not properly sampled during most hydrothermal cruises. A final list of species coming from chimney walls, vestimentiferan tubeworm clusters and mussel beds was thus compiled for nine hydrothermal vent fields: 21° N, 13° N, 11° N, 9°50' N, 7°25' S, 13°59' S, 17°25' S, 18°36' S and 21°33' S (see Appendix S1 in Supporting Information). In order to detect biogeographic relationships more precisely, given the usually non-quantitative nature of the sampling at hydrothermal vents, the data were analysed at the species presence-absence level (Desbruyères *et al.*, 2006a; Bachraty *et al.*, 2009).

Macrofaunal community structure associated with mussel beds along the SEPR (i.e. the regional scale)

Details regarding the sampling units of *B. thermophilus* are presented in Table 1. All collections were performed using the hydraulic arm of the manned submersible vehicle 'Nautile' (Ifremer). Mussels were washed on deck with filtered seawater, and the associated fauna was collected onto a 1-mm mesh sieve. The animals were sorted onboard and the retained organisms were fixed in 4% neutral formalin or in absolute ethanol for subsequent molecular analyses. In the laboratory, all specimens were sorted, identified to the lowest possible taxonomic level (i.e. mainly to the species level) under a dissecting microscope and then transferred to 70% ethanol. Data on echinoderm species correspond to those reported in Stöhr & Segonzac (2006). Large and highly motile predators, including zoarcid fishes, squat lobsters (*Munidopsis* spp.) and bythograeid crabs, together with meiofauna and vagile epifauna (mainly amphipods and copepods) were not included in the analysis. Mussels <10 mm, usually deemed to represent associated fauna at this life history stage rather than a structural component (Van Dover, 2002; Dreyer *et al.*, 2005), were also not included in the analysis. The proportion of

Table 1 Characteristics of the localities and sampling units for each *Bathymodiolus thermophilus* mussel bed sampled along the southern East Pacific Rise (SEPR). Macrofaunal density corresponds to the number of individuals standardized to the estimated surface area sampled.

Vent field	Vent sites	Latitude	Longitude	Dive	Geodynamic environment	Type of venting	No. of mussels	Size range (mm)	Proportion of juveniles (%)	Sampled area (cm ²)	Density of individuals (ind. m ⁻²)
7°25' S	Sarah's Spring (SS)	7°25.2445' S	107°47.6386' W	1574	Volcanic	Moribund	46	0–80	9	687	3959
13°59' S	Lucky Eric (LE)	13°59.2093' S	112°28.9559' W	1592	Tectonic	Diffusion	84	0–170	39	3581	1170
17°25' S	Oasis B86 (OBS6)	17°25.3843' S	113°12.2893' W	1579	Volcanic	Diffusion	147	0–170	3	8438	2028
	Rehu Marka (RM)	17°24.9787' S	113°12.1369' W	1590	Volcanic	Diffusion	91	0–160	2	11081	771
17°34' S	Susie (Susie)	17°35.4718' S	113°14.8252' W	1588	Tectonic	Chimney	607	0–170	69	9888	1794
18°36' S	Animal Farm (AF)	18°36.6966' S	113°24.0482' W	1585	Volcanic	Moribund	379	0–130	56	8735	2249
21°33' S	Grommit (Gr1)	21°33.6695' S	114°17.9049' W	1575	Tectonic	Chimney	238	10–120	0	15326	647
	Grommit (Gr2)	21°33.6648' S	114°17.9814' W	1577	Tectonic	Chimney	76	20–120	0	4823	832
	Grommit (Gr3)	21°33.6848' S	114°17.9808' W	1578	Tectonic	Chimney	430	0–120	9	11353	845

mussel specimens <10 mm, considered as juveniles, was regarded here as an indication of the mussel bed's condition (newly settled, mature or senescent mussel beds): newly settled mussel beds are expected to harbour many juveniles compared with senescent mussel beds.

The surface area (SA) of mussel shells was calculated by applying the relationship found between the mass of aluminium foil required to cover the outer surface of a mussel shell and mussel length (Bergquist *et al.*, 2005). One hundred and six mussel shells, representative of the whole size range, were used to determine this relationship. The outer shells of each collection were wrapped in aluminium foil (0.00363 g cm⁻²), and the mass required to cover the entire shell was then converted to surface area (SA). Bias emerging from folding of the aluminium foil was considered equivalent for each mussel, such that comparison between sampling units was valid. The relationship between SA (in cm²) and mussel shell length (*L*) was derived by plotting the surface area against the shell length to parameterize the following equation:

$$SA = 0.0137 L^{1.9671}.$$

This highly significant relationship ($R^2 = 0.996$; $P \leq 10^{-3}$) was then applied to each mussel collection. Standardized abundances correspond to the number of individuals divided by the area sampled and are expressed as numbers of individuals m⁻².

Barcoding of hydrothermal gastropods

The total genomic DNA was extracted using the CTAB (cetyltrimethyl ammonium bromide) procedure from ethanol-preserved specimens. Gastropods were removed from the shell, homogenized in 600 µL of a 60 °C preheated 2% CTAB buffer solution (containing 1.4 M NaCl, 0.2% 2-mercaptoethanol, 20 mM EDTA, 100 mM Tris-HCl pH 8, 0.1 mg mL⁻¹ proteinase K) and digested for 2 h at 60 °C. Proteins, lipids and carbohydrates were removed using a single chloroform-isoamyl alcohol (24:1) precipitation. DNA was precipitated with 370 µL of cold 100% isopropanol and stored at -20 °C for 1 to 2 h. The tubes were finally centrifuged at 15 000 g for 5 min. DNA pellets were washed with 70–75% ethanol and re-suspended in 20–60 µL of TE buffer (10 mM Tris-HCl; 20 mM EDTA pH 8) or sterile H₂O.

For each individual, partial sequences of the mitochondrial cytochrome *c* oxidase subunit I gene (COI) were amplified by conducting a nested polymerase chain reaction (PCR). DNA was pre-amplified with the universal primers M1 and M2 (Nelson & Fisher, 2000) and used as a target (1 µL of PCR-product) for a second amplification with the universal primers LCO1490 and HCO2198 described by Folmer *et al.* (1994). For both amplifications, the 50-µL amplification mixture contained 3 µL of template DNA, 1× PCR buffer, 2 mM MgCl₂, 0.4 µM of each primer, 10 µM of each dNTP, 2U Taq DNA polymerase, and sterile H₂O to final volume. PCRs were performed as follows: a 3-min initial denaturation step at

94 °C; 40 cycles of 45 s of denaturation at 94 °C, 45 s of annealing at 50 °C and 90 s of elongation at 72 °C; and a 7-min final elongation at 72 °C.

The PCR products were purified and sequenced on an ABI 3100 using BigDye[®] terminator chemistry (Applied Biosystems, Courtaboeuf, France) following the manufacturer's protocol. Sequences were proofread and aligned manually using BioEDIT Sequence Alignment 7.0.1 (Hall, 1999).

Phylogenetic relationships between specimens were assessed for the wide-ranging species found in large numbers in the sampling units: the lepetodrilids, namely *Lepetodrilus elevatus*, *L. cristatus*, *L. ovalis*, *L. pustulosus*, *L. tevnianus*, *Gorgoleptis emarginatus* and *G. spiralis*, the neomphalid *Pachydermia laevis*, the peltospirid *Peltospira operculata* and the neolepetopsid *Eulepetopsis vitrea*. Additional species, found in low proportions during the BIOSPEEDO cruise but well known from the EPR, were also added, namely *Nodopelta subnoda* and *Rhynchopelta concentrica* (peltospirids), and *Clypeosectus delectus* (lepetodrilid). Details of the specimens analysed are presented in Table 2. Aligned sequences were analysed using Bayesian inference. First, the optimal substitution model for COI was selected using the hierarchical likelihood ratio test (hLRT) implemented in MODELTEST 3.07 (Posada & Crandall, 1998). Then, Bayesian inferences were performed using MRBAYES 3.1.1 (Ronquist & Huelsenbeck, 2003), which uses a Markov chain Monte Carlo (MCMC) method for exploring the parameter space in a stepwise fashion. The analysis, involving six chains, was run for 10,000,000 generations with a sampling frequency of 1,000 and a burn-in period of 10,000. The trees were unrooted.

Published mitochondrial COI sequences from *Lepetodrilus elevatus* [GenBank accession numbers EU306401–EU306402 and EU306407–EU306408, described as *L. aff. elevatus* (Johnson *et al.*, 2008)], *L. pustulosus* [GenBank accession numbers EU306457–EU306458 and EU306464–EU306465 for *L. aff. pustulosus* (Johnson *et al.*, 2008)], *L. cristatus* [GenBank accession numbers EU306425–EU306426], *L. ovalis* [GenBank accession numbers EU306478–EU306479], *L. aff. galriftensis* [GenBank accession numbers EU306413–EU306414] and *L. tevnianus* [GenBank accession numbers EU306389–EU306390 and EU306395–EU306396 for *L. aff. tevnianus* (Johnson *et al.*, 2008)] were included. A published sequence of *Peltospira delicata* [GenBank accession number AY923931] was also included.

Biodiversity measurements

For both the global and regional analyses, the species richness (*S*), the average taxonomic distinctness (Δ^+) and the Jaccard coefficient were calculated from species presence-absence matrices using the DIVERSE subroutine in PRIMER 5 (Clarke & Warwick, 2001).

The average taxonomic distinctness (Δ^+) is the average taxonomic distance between all pairs of species (*i* and *j*) in a sampling unit, from tracing these distances through a taxonomic tree such as (Warwick & Clarke, 2001):

Table 2 List of gastropod species from the East Pacific Rise (EPR) used in the barcoding analysis. The number of specimens per locality is given in parentheses.

Species	This study	GenBank accession numbers
<i>Eulepetopsis vitrea</i>	21° N (1), 13° N (1), 9°50' N (1), 7°25' S (1), 13°59' S (1), 17°25' S (1), 17°34' S (1), 18°36' S (1), 21°33' S (1)	
<i>Lepetodrilus elevatus</i>	21° N (1), 13° N (2), 13°59' S (1), 17°25' S (1), 17°34' S (1), 21°33' S (4)	EU306401–402 (Wood: 22° N/EPR:21° N–0°)
<i>Lepetodrilus</i> aff. <i>elevatus</i>		EU306407–408 (EPR:7° S–38° S)
<i>Lepetodrilus</i> aff. <i>galrifiensis</i>		EU306413–414 (EPR:9° N–23° S)
<i>Lepetodrilus ovalis</i>	7°25' S (1), 13°59' S (1), 17°25' S (1), 17°34' S (1), 18°36' S (1), 21°33' S (1)	EU306478–479 (EPR:Monterey Bay/EPR:21° N–38° S)
<i>Lepetodrilus pustulosus</i>	13° N (3)	EU306457–458 (Wood:22° N/EPR:21° N–17° S)
<i>Lepetodrilus</i> aff. <i>pustulosus</i>		EU306464–465 (EPR:31° S–38° S)
<i>Lepetodrilus tevnianus</i>		EU306389–390 (EPR:9° N–23° S)
<i>Lepetodrilus</i> aff. <i>tevnianus</i>		EU306395–396 (EPR:23° S–31° S)
<i>Lepetodrilus cristatus</i>	13° N (17)	EU306425–426 (EPR:21° N–38° S)
<i>Gorgoleptis emarginatus</i>	7°25' S (2), 13°59' S (1), 17°25' S (2), 21°33' S (1)	
<i>Gorgoleptis spiralis</i>	14° S (1), 17°24' S (2), 21° 33' S (3)	
<i>Clypeosectus delectus</i>	17°25' S (2), 21°33' S (1), 23° S (2)	
<i>Pachydermia laevis</i>	21° N (3), GoC (1), 13° N (1), 17°25' S (2), 17°34' S (1), 18°36' S (2), 21°33' S (2), 31° S (1)	
<i>Peltoispira operculata</i>	13° N (4), 13°59' S (2), 17°25' S (1), 17°34' S (1), 18°36' S (2), 21°33' S (2)	
<i>Peltoispira delicata</i>		AY923931
<i>Nodopelta subnoda</i>	13° N (2)	
<i>Rhynchopelta concentrica</i>	13° N (2)	

$$\Delta^+ = [\sum_{i < j} \omega_{ij}] / [S(S-1)/2],$$

where ω_{ij} is the 'distinctness weight' given to the path-length linking species i and j in the hierarchical classification, S is the total number of species in the sampling unit, and the double sum is over all pairs of species. Five taxonomic levels were considered: species, genus, family, order and class. As equal step-lengths were assumed between successive taxonomic levels and the path-length ω was set to 100 for two species connected at the highest taxonomic level, the weights are $\omega_{ij} = 20$ (species in the same genus), 40 (same family but different genera), 60 (same order but different families), 80 (same class but different orders) and 100 (different classes). For semi-quantitative collections performed in mussel beds along the SEPR, this index was then tested by comparing the observed values to the distribution of the expected values of Δ^+ under the null hypothesis that sampling units are a random collection of the regional species pool. These expected values were generated for a given number of species (S) after 1000 re-samplings of the dataset for each S -value. The regional species list is that of the species found in mussel beds along the whole SEPR, adding species from this study and from Van Dover (2002, 2003). In the context of this study, the main advantage of this index is that it is independent of sample size and sampling effort.

Pielou's evenness (J'), the Shannon–Wiener diversity index (H') and the rarefaction index $ES_{(n)}$ were calculated for each mussel bed sampling unit from species relative abundance matrices using the DIVERSE subroutine in PRIMER 5. The $ES_{(n)}$

rarefaction index estimates the expected number of species (ES) in normalized sampling units of n individuals from a larger real sample of S species and N individuals (Hurlbert, 1971). It was originally designed to allow comparisons of species diversity from sampling units of very different size. This method assumes that sampling units are homogeneous with similar distributions of individuals among species and that the species are randomly distributed. These assumptions are rarely observed in practice, so the rarefaction index will be strongly biased for small samples. In our case, the sampling units were normalized to the smallest common number of individuals, that is, to the 600 found at Grommit (21°33' S) (Table 1).

Multivariate statistical analyses

Prior to multivariate analyses, a Hellinger transformation was applied to the species' response data. The transformation consists of dividing each species' presence value by the total number of species at the site, or the abundance by the sum of the species present at the site, and then taking the square root of the ratio. After this transformation, Euclidean methods of analysis such as multivariate regression tree (MRT) and canonical redundancy analysis (RDA) (described below) will preserve the Ochiai distance among sites for presence–absence data, or the Hellinger distance among sites for abundance data. These distances are more appropriate than the Euclidean distance for ordination or MRT analysis of community

composition data (Legendre & Gallagher, 2001). All calculations were performed through R language functions (R Development Core Team, 2006).

Global analysis of communities along the EPR

For the global analysis, putative biogeographic breaks were identified using a multivariate regression tree (MRT) (De'ath, 2002) computed for two different datasets: (1) the species list recorded in Desbruyères *et al.* (2006b), and (2) that list completed with the species collected during the BIOSPEEDO cruise (Appendix S1). This method was used to define groups of fields that are similar in faunal composition while geographically adjacent. The MRT is a partitioning method of the multivariate response data table (i.e. species) constrained in the present study along the axis of a single explanatory variable (i.e. latitude) to generate spatially consistent groups of neighbouring fields. The tree structure is generated by partitioning the whole dataset into mutually exclusive groups. It is grown by successive binary splits of the data, each split involving a breakpoint in the latitude variable. Each split is chosen to minimize the total multivariate sum of squares within the two groups formed, or to maximize the R^2 (or equivalently the among-group sum-of-squares) at each division step. The tree with the lowest cross-validation error is chosen as the best predictive tree. At the end of the procedure, each leaf of the tree is characterized by a number of sites, the multivariate mean of the sites, and the explanatory variable values that define it. The tree was computed using the 'mvpart' library (De'ath, 2002) in the R statistical language (R Development Core Team, 2006).

Because the latitudinal gradient is bounded by geographic barriers (i.e. the North American plate in the north and the Easter Island microplate in the south, Fig. 1), the species distribution was compared with predicted data according to the geometry theory of species richness (Colwell & Lees, 2000). In response to geometric constraints, mid-domain effect (MDE) models predict for a bounded geographic domain a convex, symmetrical pattern of species richness in the absence of any additional environmental effect or other gradient. The predicted species richness was computed using RANGEModel 5 (R.K. Colwell, <http://viceroy.eeb.uconn.edu/rangemodel>) following the one-dimensional discrete null model developed by Dunn *et al.* (2006) to account for gaps in species ranges. The 95% confidence interval was computed after 9999 randomizations. To assess the role of MDE on species richness, we computed an MRT using the species richness values predicted by the MDE null model as an explanatory variable in addition to the previously used geographic variable.

Variation of the macrofaunal community structure associated with mussel beds along the SEPR

To investigate the correlations of faunal composition with explanatory variables and identify putative geographic breaks, a canonical redundancy analysis (RDA) and an MRT were

computed on the Hellinger-transformed abundance data of the macrofauna associated with mussel beds along the SEPR. The RDA combines aspects of ordination and regression and uses a permutation procedure to test the significance of the explained variation; thus species abundances do not have to be normally distributed (Legendre & Legendre, 1998). The explanatory variables were the latitude from the equator, the geodynamic environment (two-state variable: tectonic versus volcanic), the type of venting (three-state variable: 1 = moribund, 2 = diffusion zone, 3 = chimney wall) and the proportion of juvenile mussels (i.e. <10 mm). Forward selection of the environmental variables was conducted to select a parsimonious model. Permutation tests involving 999 random permutations were run to test the significance of the canonical relationship and of the individual canonical axes. The redundancy analysis was computed using the `rdaTest()` function of the 'rdaTest' package available on the page <http://www.bio.umontreal.ca/legendre/>.

In order to group the sampling units collected from the mussel beds according to their faunal composition, the chord distance was calculated between the sampling units from the relative species abundance data. This measure is similar to the Euclidean distance after normalization of the site vectors and is thus more appropriate when the sampling area is variable among sampling units. The sites were then clustered using the unweighted pair-group method using arithmetic averages (UPGMA). This method was chosen because it gave the highest correlation between the chord distances and the cophenetic matrix corresponding to the dendrogram (i.e. containing the levels at which sampling sites *i* and *j* become members of the same cluster). Hierarchical clustering was computed using the `hclust()` function of the 'stats' package in R.

RESULTS

Global analysis of the vent fauna along the EPR

The BIOSPEEDO cruise added 18 species to the list reported in Desbruyères *et al.* (2006b), leading to a final list of 96 species along the whole EPR (Appendix S1). Data acquired during the BIOSPEEDO cruise extended the geographic range of most gastropod and polychaete species that had been previously reported from the northern EPR (Warén & Bouchet, 2001; Desbruyères *et al.*, 2006b). As an example, *Lepetodrilus tevnianus*, recorded previously only at 11° N, was collected at 13°59' S, 17°25' S and 21°33' S. *Lepetodrilus cristatus*, previously recorded at 21° N, 13° N and from the Galápagos, was found at 13°59' S and 21°33' S. Similarly, *Echinopelta fistulosa* and *Cyathernia naticoides*, known only from the northern EPR (i.e. 9° N to 21° N), were collected at 21°33' S and 17°25' S, respectively. Furthermore, this cruise led to the discovery of 10 new morphospecies: *Phymorhynchus* n. sp. at 17°25' S and 18°36' S, *Melanodrymia* n. sp. and *Haloceras* n. sp. at 21°33' S for gastropods (A. Warén, pers. obs.); *Paralvinella* n. sp., *Glycera* n. sp. and a new Ampharetidae species at 21°33' S; *Sphaerodopsis* n. sp. at 18°36' S; *Nicomache* n. sp. and a new species of Flabelligeridae at 17°25' S and 21°33' S; and *Oasisia*

Table 3. Diversity indices for each hydrothermal vent field along the East Pacific Rise (EPR), computed from presence–absence data of macrobenthic invertebrate species. EPR handbook, data reported in the *Handbook of deep-sea hydrothermal vent fauna* (Desbruyères *et al.*, 2006b); EPR hb+bs, species collected along the southern EPR during the BIOSPEEDO cruise (bs) were added to the handbook data (hb). S, species richness; Δ^+ , average taxonomic distinctness.

Vent site	EPR handbook		EPR hb+bs	
	S	Δ^+	S	Δ^+
21° N	51	79.79	51	79.79
13° N	62	80.94	62	80.94
11° N	42	80.22	42	80.22
9°50' N	45	79.41	45	79.41
7°25' S	21	78.73	35	79.33
13°59' S	22	79.73	34	79.32
17°25'–34' S	28	84.48	60	81.96
18°36' S	14	79.3	38	83.95
21°33' S	13	76.5	52	80.62

n. sp. between 7°25' S and 17°25' S for polychaetes (D. Desbruyères & S. Hourdez, pers. obs.). *Haloceras* is also a new genus for hydrothermal vents. These new species were found only south of latitude 17°25' S. Two species that belong to genera characterizing other ridge systems (i.e. *Eosipho auzendi* from the Pacific Antarctic Ridge and *Shinkailepas* sp., a genus previously known from the MAR and back-arc basins) were also reported. Moreover, the gastropods *Nodopelta heminoda* and *N. subnoda* and the polychaete *Hesiolyra bergi*, highly abundant on the chimney walls of the NEPR vent fields, were virtually absent (very few individuals) from SEPR sampling units, despite an intense sampling effort (nine chimneys extensively sampled).

When analysing only the species dataset reported in the *Handbook of deep-sea hydrothermal fauna* (Desbruyères *et al.*, 2006b), species richness was twice as high at all NEPR vent fields (i.e. 42 to 62 species) as at any vent field on the SEPR (i.e. 13 to 28 species) (Table 3). The highest species richness was observed at 13° N and 21° N (i.e. 62 and 51, respectively) for the NEPR and at 17°25' S (i.e. 28) for the SEPR. Average taxonomic distinctness was nearly homogeneous along the whole EPR, with the highest value (84.48) found at 17°25' S. Adding the species sampled during the BIOSPEEDO cruise significantly increased the number of species recorded on the SEPR to values similar to the ones on the NEPR. The analysis revealed two centres of species diversity: one in the north including 21° N and 13° N, and one in the south comprising the vent fields between 17°25' S and 21°33' S. Species richness on the SEPR reached 60 at 17°25' S as opposed to 62 at 13° N. The average taxonomic distinctness was not affected greatly, with the highest value still found along the SEPR (Table 3). The empirical species richness does not display a mid-domain peak as predicted under the MDE model. Indeed, six out nine hydrothermal vent fields fell outside the 95% confidence interval of values predicted by the model (Fig. 2).

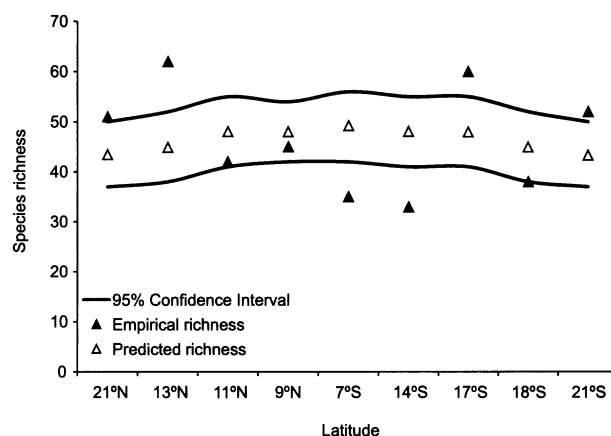


Figure 2 Empirical (black triangles) and predicted (open triangles) species richness of macrobenthic invertebrate communities along the East Pacific Rise. The 95% confidence intervals, indicated by the lines, are based on 9999 randomizations of range placement for the set of empirical range sizes, taking distributional gaps into account.

The multiple cross-validations produced an MRT with three groups of fauna for both analyses, explaining 70.3% of the variation in the species dataset when considering only the handbook data and 45.4% when adding the new species records (Fig. 3). Those trees displayed the lowest cross-validation error and offered sufficient resolution when considering the number of observed hydrothermal fields along the EPR (i.e. 9). The first split separated the northern and southern parts of the EPR near the equator. A second split subdivided the SEPR into two groups of assemblages: south of latitude 17°35' S when considering only the species reported in the handbook; and south of latitude 13°59' S when the species collected during the BIOSPEEDO cruise were added to the analysis. Adding the predicted species richness under the MDE model as an explanatory variable did not improve the tree resolution (detailed results not shown).

Evidence of species crypticism and vicariance in vent gastropods

Phylogenetic relationships were analysed for 14 species of Lepetodrilidae, Neolepetopsidae, Neomphalidae and Peltospiridae gastropods along the whole EPR using a 425-bp sequence portion of the cytochrome *c* oxidase subunit I (COI). The COI sequences correspond to the accession numbers from GU984234 to GU984303 in GenBank. The tree obtained by Bayesian inference is presented in Fig. 4. All nodes with a probability less than 95% were collapsed to a basal polytomy. Within the Lepetodrilidae family we detected 13 clades, with 10 clades involving five species of the genus *Lepetodrilus*. The two species of the genus *Gorgoleptis*, *Lepetodrilus cristatus* and *Clypeosectus delectus* were the only species not subdivided into two sister clades. However, both the *Gorgoleptis* and *Clypeosectus* species were collected only from the SEPR, while only *L. cristatus* individuals from 13° N were available for molecular

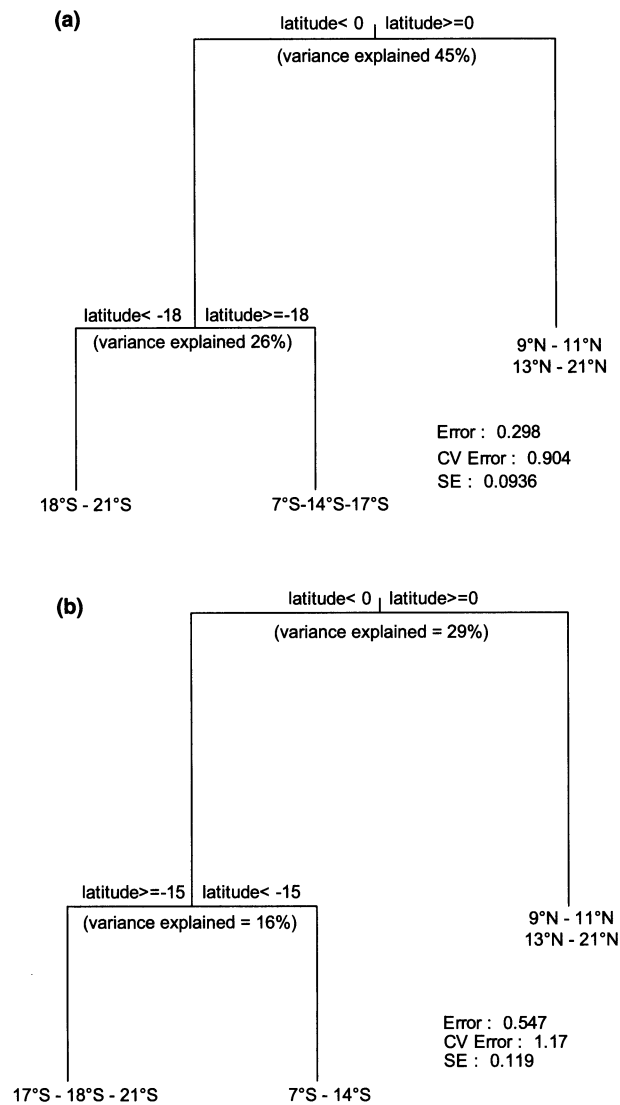


Figure 3 Groups obtained by multivariate regression tree analysis of presence-absence data along the East Pacific Rise. Negative latitudes shown on the splits are south of the equator. (a) Data from the *Handbook of deep-sea hydrothermal vent fauna* (Desbruyères *et al.*, 2006b). (b) Species list complemented with data from the BIOSPEEDO cruise.

analysis. Pairwise K2P distances (Kimura, 1980) between clades detected within each well-identified morphological species (*L. elevatus*, *L. pustulosus*, *L. ovalis*, *L. cristatus* and *L. tevnianus*) ranged between 1.5 and 8.3%. Within cryptic lineages (i.e. clades), pairwise distances ranged from 0 to a maximum of 1.5%. *Lepetodrilus* aff. *galriftensis*, identified by Johnson *et al.* (2008), grouped with the southern clade (9°50' N to 21°33' S) of *L. elevatus* (Matabos *et al.*, 2008a; Plouviez *et al.*, 2009), and *Lepetodrilus* aff. *elevatus* (Johnson *et al.*, 2008) with the third clade found only at 21°33' S. This latter clade diverged from the northern and southern clades by 7 and 5.8% respectively. *Lepetodrilus ovalis* also displayed two clades with a slight divergence of 1.5%. The two clades of *L. tevnianus* and *L. pustulosus* diverged by 6.2 and 9.2%,

respectively. In Neolepetopsidae, *Eulepetopsis vitrea* also displayed two distinct geographic mitochondrial lineages, separated by a divergence of 1.5% and located on either side of the equator. Within the Peltospiridae and Neomphalidae, *Peltospira operculata* and *Pachydermia laevis* exhibited two to three divergent clades. *Peltospira operculata* and *Pachydermia laevis* showed the strongest divergence between the NEPR and SEPR, with 7.9 and 12.5% divergence between the two clades, respectively. An individual of *P. laevis* sequenced from 31° S beyond the Easter microplate showed 10.8% divergence from the NEPR clade and 11.2% from the SEPR. For those two species, pairwise K2P distances within cryptic clades ranged from 0.2 to 0.6%.

Except for *L. ovalis*, cryptic lineages within a single morphological species were geographically structured with a northern and southern lineage across the equator and, in a few cases, an additional mitochondrial lineage in the southernmost vent field (i.e. 21°33' S). The absence of sampling units between 9°50' N and 17°25' S for several taxa makes a clear identification of the location of the geographic break along the ridge impossible. Furthermore, as it was impossible to identify lineages on the basis of morphological criteria, the species complexes identified here were not subjected to further biogeographic analyses.

Variations in the macrofaunal community structure of mussel beds along the SEPR

A total of 13,339 individuals belonging to 61 species were collected in mussel beds along the SEPR: 28 species of gastropods (19 genera and 11 families), 31 species of polychaetes (22 genera and 15 families), and 2 species of echinoderms (2 genera and 2 families) (Table 4). The most abundant species at the regional scale were *Lepetodrilus* spp. (i.e. *L. elevatus* and *L. ovalis*), *Eulepetopsis vitrea*, *Amphisamytha galapagensis* and *Archinome rosacea*. While *Melanodrymia aurantiaca* was found only at 21°33' S, it was highly abundant at that site, because mussels colonized an active black smoker. By contrast, *Planorbidella* cf. *planispira* was found in most sampling units but with few individuals at each locality. Local species richness varied between 11 and 27, with the lowest values observed at Lucky Eric (13°59' S), Susie (17°34' S) and Sarah's Spring (7°25' S) (Table 5). The highest species diversities, in terms of both species richness and rarefaction index, were observed at the 17°25' S Rehu Marka, 18°36' S Animal Farm and 21°33' S Grommit sites. However, Shannon indices are relatively low, ranging between 0.53 at Susie and 2.40 at Rehu Marka (Table 5).

The average taxonomic distinctness index Δ^+ varied between 67.20 for Lucky Eric (13°59' S) and 88.84 for Animal Farm (18°36' S). The other highest values, observed for collections at Oasis (17°25' S), Rehu Marka (17°25' S) and Grommit (21°33' S), were equivalent. Oasis (17°25' S), Rehu Marka (17°25' S), Animal Farm (18°36' S) and one replicate from Grommit (i.e. Gr2, 21°33' S) were significantly higher than the theoretical value estimated by 1000 permutations of the

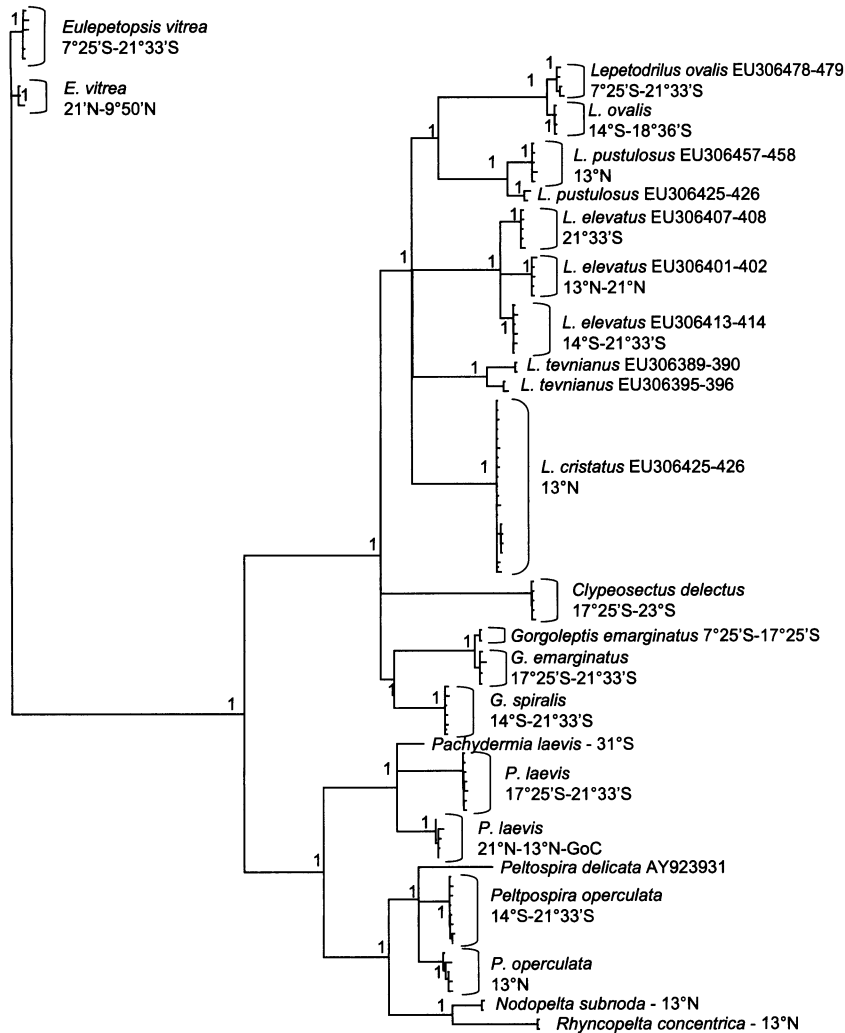


Figure 4 Phylogenetic relationships among 14 species of gastropods along the East Pacific Rise (COI sequences of 111 individuals) computed by Bayesian inferences. Numbers along the tree correspond to the posterior probability values of the nodes. GenBank sequences added to the tree were provided by Johnson *et al.* (2008). Site abbreviations are as in Table 1.

0.1

dataset. The sampling unit collected at Lucky Eric (13°59' S) was significantly smaller in terms of average taxonomic distinctness (Fig. 5).

The UPGMA dendrogram in Fig. 6 shows a clear separation of sampling sites into three distinct groups, plus one isolated site, namely Sarah's Spring (7°25' S). Sarah's Spring is characterized by low species richness and taxonomic diversity, with the absence of echinoderms and the presence of six species of polychaetes. This site differs from others because the gastropod *Lepetodrilus pustulosus*, virtually absent from other sampling units, was found in high numbers. Together *Lepetodrilus pustulosus* and the polychaete *Amphisamytha galapagensis* accounted for 85% of the individuals collected. The first group on the dendrogram corresponds to the highest values of the Shannon diversity index and high average taxonomic distinctness (Table 5). It includes Animal Farm (18°36' S) and Rehu Marka (17°25' S), which contained five and seven dominant species, respectively (i.e. >5% of individuals). The second group, which includes collections from Lucky Eric (13°59' S), Oasis BS6 (17°25' S) and Susie (17°34' S), had the

lowest Shannon diversity index (Table 5). These collections are composed mainly of lepetodrilid species, with *L. elevatus* present at levels of up to 88 and 90% in the sampling units collected at Oasis BS6 and Susie, respectively. Finally, sampling units collected at Grommit (21°33' S) formed a single group with 65% species similarity. They displayed the same species and taxonomic diversity and contained at least three new species each, five new species shared only by these sampling units (i.e. *Melanodrymia* n. sp., *Glycera* n. sp., *Nichomache* n. sp., *Oasisia* n. sp. and the new species of Ampharetidae) and one new species for the EPR (i.e. *Shinkailepas* sp.).

The sites and the explanatory variables used in the RDA are displayed in an ordination biplot in Fig. 7. The results of the RDA showed that, after forward selection, the transformed species abundances were significantly correlated with two environmental variables out of four: the latitude and the type of venting (i.e. moribund state) ($R^2_{\text{adj}} = 0.28$, $P = 0.0004$). The first axis accounted for 27.6% ($P = 0.001$) of the total variation in species abundance data. The biplot also shows the four groups of fields from Fig. 6. The MRT analysis produced

Table 4 List of macrobenthic invertebrate species of the communities associated with nine *Bathymodiolus thermophilus* mussel beds sampled along the southern East Pacific Rise (SEPR).

Taxon	Family	Species	Sarah's Spring (7°25' S)	Lucky Eric (13°59' S)	Oasis BS6 (17°25' S)	Rehu Marka (17°25' S)	Susie (17°34' S)	Animal Farm (18°36' S)	Grommit (1) (21°33' S)	Grommit (2) (21°33' S)	Grommit (3) (21°33' S)
Gastropods	Neolepetopsidae	<i>Eulepetopsis vitrea</i>	291	170	20	76	41	449	10	6	21
	Trochidae	<i>Bathymargarites simplex</i>	15	0	8	7	0	260	0	0	0
	Sutizonidae	<i>Sutizona theca</i>	0	0	0	0	0	0	2	0	0
	Lepetodrilidae	<i>Lepetodrilus elevatus</i>	15	757	1791	19	1607	2	42	29	102
		<i>Lepetodrilus pustulosus</i>	1877	64	0	0	6	0	0	0	2
		<i>Lepetodrilus ovalis</i>	87	103	63	219	114	218	11	12	57
		<i>Lepetodrilus cristatus</i>	0	25	0	0	2	0	5	10	4
		<i>Lepetodrilus tevianus</i>	0	17	0	0	4	0	1	2	2
	Gorgolettidae	<i>Gorgolettis cf. emarginatus</i>	73	3	0	17	1	0	0	0	5
		<i>Gorgolettis spiralis</i>	15	8	32	48	0	10	5	12	15
		<i>Gorgolettis patulus</i>	0	0	1	0	0	0	0	0	0
		<i>Glypeosectus</i> sp.	58	0	14	23	0	0	0	2	0
		<i>Cyathiermia naticoides</i>	0	0	0	0	0	0	0	0	0
Neomphalidae	Neomphalidae	<i>Melanodrymia auriantica</i>	0	0	0	0	0	0	472	309	458
		<i>Melanodrymia galeronae</i>	0	0	0	0	0	0	1	0	0
		<i>Melanodrymia</i> n. sp.	0	0	0	0	0	0	1	0	0
		<i>Pachydermia</i> cf. <i>laevis</i>	0	0	0	33	0	0	18	6	20
		<i>Planorbicella</i> cf. <i>planispira</i>	0	3	17	29	2	18	2	2	12
	Peltospiroidae	<i>Neomphalus fretterae</i>	0	0	1	0	0	1	0	0	0
		<i>Nodopelta subnoda</i>	0	0	0	0	0	0	0	15	0
		<i>Echinopelta fistulosa</i>	0	0	0	0	0	0	0	149	0
		<i>Rhynchopelta concentrica</i>	0	0	0	0	2	0	0	0	0
		<i>Shinkalepas</i> sp.	0	0	0	0	0	0	0	4	0
	Phenacolepidae	<i>Provanna</i> sp.	0	0	0	0	0	0	0	0	0
		<i>Phymorhynchus</i> n. sp.	0	0	2	0	0	2	0	0	0
		<i>Phymorhynchus</i> cf. <i>major</i>	0	0	0	0	0	0	0	0	0
		<i>Laeviphius</i> sp.	0	0	0	1	0	0	0	0	0
		<i>Eosipho auzendi</i>	0	0	0	0	0	6	0	0	4
Polychaetes	Amphinomidae	<i>Archinome rosacea</i>	0	0	15	134	0	389	21	70	25
		<i>Ophryotrocha akessoni</i>	0	0	4	4	0	22	0	50	15
		<i>Glycera</i> n. sp.	0	0	0	0	0	0	0	0	1
		<i>Hesiospina vestimentifera</i>	0	0	0	52	0	332	1	10	0
		<i>Hesiolira bergi</i>	0	0	0	0	0	0	1	0	0
	Nereididae	<i>Hesioeca</i> cf. <i>hessleri</i>	0	0	0	26	0	0	0	0	0
		<i>Nereis andersi</i>	0	0	3	10	0	68	26	46	13
	Nereididae										

Table 4 Continued

Taxon	Family	Species	Sarah's Spring (7°25' S)	Lucky Eric (13°59' S)	Oasis BS6 (17°25' S)	Rehu Marka (17°25' S)	Susie (17°34' S)	Animal Farm (18°36' S)	Grommit (1) (21°33' S)	Grommit (2) (21°33' S)	Grommit (3) (21°33' S)
(Polychaetes)	Phyllodoctidae	<i>Galapagomystides aristata</i>	0	0	0	0	0	2	0	0	0
	Polynoidae	<i>Branchipolynoe symmytilda</i>	20	20	56	2	23	96	10	5	14
		<i>Branchinotogluma hessleri</i>	0	0	0	1	0	0	0	0	0
		<i>Branchinotogluma sandersi</i>	0	0	0	0	0	0	0	0	0
		<i>Levensteiniella kincaidi</i>	15	0	14	18	0	0	0	10	2
		<i>Levensteiniella plicata</i>	0	0	0	1	0	10	1	0	0
		<i>Lepidonotopodium fimbriatum</i>	29	0	0	0	0	0	1	10	3
		<i>Lepidonotopodium williamsae</i>	29	0	4	1	0	0	0	0	0
		<i>Lepidonotopodium atalantae</i>	0	0	1	0	0	0	0	0	0
		<i>Thermiphone tufari</i>	0	0	1	2	0	21	3	4	2
		<i>Laminatubus alvinus</i>	0	0	4	0	0	0	0	0	0
	Serpulidae	<i>Oasiasia n. sp.</i>	0	17	1	0	0	0	0	0	0
	Siboglinidae	<i>Riftia pachyptila</i>	0	0	1	0	4	0	0	0	0
		<i>Tevnia jerichonana</i>	0	0	0	0	0	0	0	2	0
		<i>Nicomache n. sp.</i>	0	0	8	0	0	0	2	6	1
		<i>Prionospio sp.</i>	0	0	1	0	0	0	3	6	0
Echinoderms	Flabelligeridae	<i>Flabelligeridae n. sp.</i>	0	0	1	0	0	2	0	2	0
	Sphaerodoridae	<i>Sphaerodoropsis n. sp.</i>	0	0	0	0	0	40	0	0	0
		<i>Alvinella caudata</i>	0	0	0	0	0	0	1	0	0
	Alvinellidae	<i>Paralvinella n. sp.</i>	0	0	0	0	0	0	0	28	0
		<i>Paralvinella pandorae</i>	0	0	0	4	1	0	0	0	0
		<i>Paralvinella grasslei</i>	2	0	0	0	0	0	0	0	0
		<i>Amphisamytha galapagensis</i>	1455	0	18	36	10	229	14	41	78
	Ampharetidae	<i>Ampharetidae n. sp.</i>	0	0	0	0	0	0	1	0	1
	Ophiuridae	<i>Spinophiura jolliveti</i>	0	0	0	0	0	151	0	0	0
		<i>Ophiolamina eprae</i>	0	0	1	1	0	6	0	0	0

Table 5 Diversity indices for each semi-quantitative sample collected in *Bathymodiolus thermophilus* mussel beds along the southern East Pacific Rise. *N*, number of individuals m^{-2} ; *S*, species richness; $ES_{(600)}$, rarefaction index based on a sampling unit size of 600 individuals; J' , Pielou's evenness; H' , Shannon-Wiener diversity index; Δ^+ , average taxonomic distinctness.

Vent field	Vent site	<i>N</i> (ind. m^{-2})	<i>S</i>	$ES_{(600)}$	J'	H' (\log_e)	Δ^+
7°25' S	Sarah's Spring	3981	14	12.88	0.50	1.32	75.45
13°59' S	Lucky Eric	1187	11	10.76	0.53	1.27	67.20
17°25' S	Oasis -BS6	2082	26	17.48	0.23	0.75	87.02
17°25' S	Rehu Marka	773	25	23.78	0.75	2.40	86.01
17°34' S	Susie	1817	13	9.81	0.20	0.53	77.09
18°36' S	Animal Farm	2343	24	19.91	0.73	2.32	88.84
21°33' S	Grommit (Gr1)	655	25	24.22	0.40	1.29	84.6
21°33' S	Grommit (Gr2)	848	27	26.58	0.68	2.26	86.28
21°33' S	Grommit (Gr3)	858	24	22.39	0.56	1.79	84.2

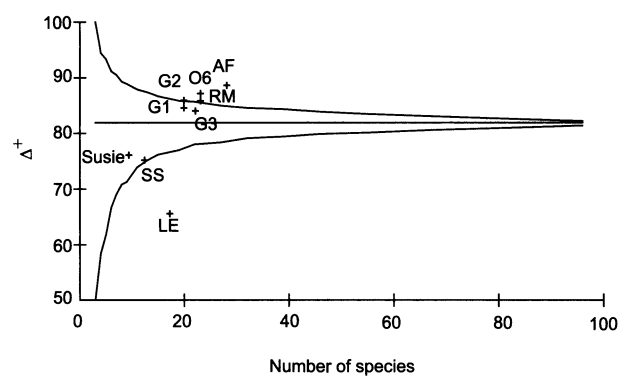


Figure 5 Computed values of average taxonomic distinctness (Δ^+) from the semi-quantitative sampling units collected in the mussel beds along the southern East Pacific Rise, plotted against the number of species on the simulated 95% confidence interval generated after 1000 re-samplings of the same number of species from the total southern East Pacific Rise species list. Site abbreviations are as in Table 1.

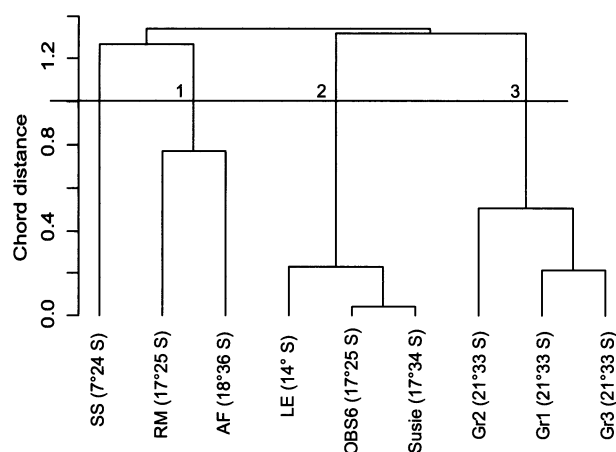


Figure 6 Group-average sorting (UPGMA unweighted pair-group method using arithmetic averages) dendrogram computed from the chord distance among the nine sampling units collected in mussel beds along the southern East Pacific Rise. Numbers identify clusters. Site abbreviations are as in Table 1.

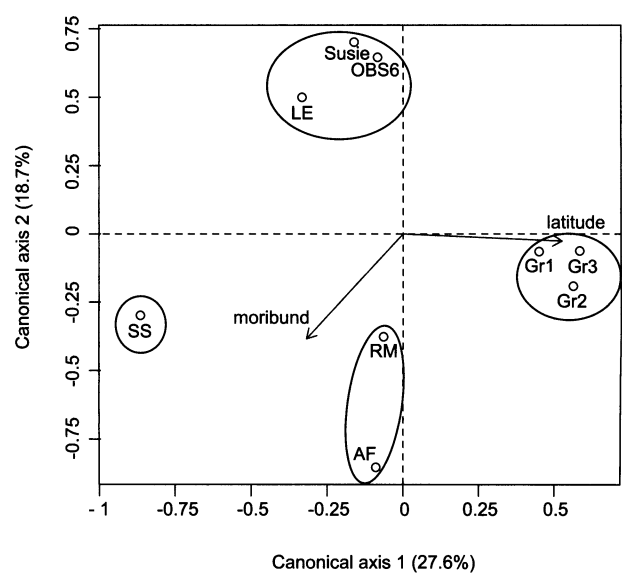


Figure 7 Redundancy analysis ordination correlation biplot of the sites and environmental variables based on the transformed species abundance of macrobenthic invertebrate communities associated with mussel beds along the southern East Pacific Rise. Site abbreviations are as in Table 1. Groups identified in the dendrogram (Fig. 6) are represented with ellipses. Environmental variables: latitude and type of venting (i.e. moribund). Species are not represented.

exactly the same patterns of faunal distributions as that obtained from the global analysis performed along the whole EPR from the presence-absence dataset (results not shown).

DISCUSSION

The specialized nature of vents and their geographic isolation on active spreading centres are interesting features for the study of vicariance, species dispersal and colonization pathways (Tunncliffe, 1988). Two complementary approaches are commonly used in biogeography: historical and ecological biogeography. While ecological biogeography investigates the current mechanisms of communication and dispersion at the

regional scale, historical biogeography studies the role of tectonic/climatic events that have led to the formation or dislocation of geographic barriers. When considering oceanic ridges at a global scale, tectonic events, creating physical barriers such as transform faults or microplates, can lead to the isolation of species in allopatry (i.e. vicariant species). This process has been suggested to be an important driving force of vent fauna evolution (Tunncliffe & Fowler, 1996; Tunncliffe *et al.*, 1998). Ecological biogeography studies the factors that define the spatial distributions of species at the present time, and thus the processes acting at regional to local scales (Monge-Najera, 2008). Local factors do not act only at the community level – they can have broader significance. As an example, at the vent scale, spatial habitat heterogeneity, related to spatial variation in fluid fluxes, results in the occurrence of multiple microhabitats at the centimetre scale (Sarrazin *et al.*, 1997; Mills *et al.*, 2007) and could promote sympatric speciation. This process, also called ecological speciation, has been suggested to fix divergence *c.* 20 times faster than species formation in allopatry but is rarely observed in nature (Via, 2001; Briggs, 2006). On the other hand, local processes influencing community structure and biodiversity patterns can blur broader biogeographic patterns if a non-adapted sampling strategy is used (e.g. too few sampling units and/or replicates, given the scope of the study). Ecology and biogeography are thus complementary approaches for understanding biodiversity patterns (Briggs, 2007).

Evidence of crypticism in gastropod species

For the lepetodrilid species, 6.5% divergence has already been shown for *L. elevatus* between the northern and southern clades found in sympatry at 9°50' N (Matabos *et al.*, 2008a). Johnson *et al.* (2008) also revealed several distinct cryptic species complexes within the genus *Lepetodrilus*, with pairwise COI distances ranging between 4.37 and 31.25%. *Pachydermia laevis* displayed haplotypes with 12.5% divergence between the northern and southern EPR, which is higher than the divergence found from individuals collected on the other side of the Easter microplate. The level of sequence divergence between haplotypes of *Peltoispira operculata* found on either side of the equator fell in the same range as that of the lepetodrilids, with 7.9% divergence. Moderate genetic divergences (0.9 to 1.5%) between geographically structured northern and southern EPR populations were detected for other taxonomic groups, including bivalves and polychaetes (Plouviez *et al.*, 2009). While levels of divergence can be highly variable between sets of sibling species (Knowlton, 2000), the pairwise genetic distances between and among clades highlighted in this study fit inter- and intra-specific levels previously described from closely related species (Peck *et al.*, 1997), highlighting the occurrence of two new cryptic species complexes along the EPR, namely *Pachydermia laevis* and *Peltoispira operculata*. Since the development of molecular techniques, the occurrence of sibling species appears to be more widespread than previously thought in hydrothermal

ecosystems, and at a broader scale, in the sea (Knowlton, 2000; Johnson *et al.*, 2008; Matabos *et al.*, 2008a; Vrijenhoek, 2009).

Biogeographic entities along the EPR

The barcoding of hydrothermal species (Johnson *et al.*, 2008), population genetics studies (e.g. Chevaldonné *et al.*, 2002; Won *et al.*, 2003; Hurtado *et al.*, 2004; Matabos *et al.*, 2008a) and comparative phylogeography (Plouviez *et al.*, 2009) along the EPR all point to the existence of a genetic break near the equator at the scale of the whole vent community. Several topographic features, related to ridge history, have been proposed to explain the divergence observed between cryptic species. The formation of the Bauer microplate, 17–6 Ma (Matabos *et al.*, 2008a), and the fossilization of the Mathematician ridge (Plouviez *et al.*, 2009) at about the same time have been proposed to account for the divergence observed in the split of *L. elevatus* into two cryptic lineages. Four out of five lepetodrilid species display the same range of genetic divergence (i.e. 5.2 to 9.2%; Johnson *et al.*, 2008; Matabos *et al.*, 2008a; this study) and may thus share the same history. However, levels of divergence are variable among species, with two sets of values ranging from 6 to 12% (an 'old' vicariant event involving *L. elevatus*, *L. pustulosus*, *L. tevnianus*, *Peltoispira operculata* and *Pachydermia laevis*) and from 1.5 to 3% (a more 'recent' tectonic event at the equator involving *E. vitrea* but also *Alvinella pompejana*, *Bathymodiolus thermophilus* and *Hesiolyra bergi*; see Plouviez *et al.*, 2009). Tests on shared divergence times performed on seven hydrothermal vent species along the EPR by Plouviez *et al.* (2009) revealed the occurrence of a common vicariant event *c.* 1.3 Ma for all studied species, including *L. elevatus*, for which another older speciation event is also detected *c.* 11.5 Ma. These latter authors therefore proposed that the formation of transform faults *c.* 1 to 2 Ma between 4° S and 14° S may be responsible for this vicariant break and the emergence of a transition zone in this area.

Analyses of community composition expressed in terms of presence-absence support the molecular dataset. Recently, Bachraty *et al.* (2009) suggested that the EPR is divided into two biogeographic provinces: the NEPR and the SEPR. Our MRT analyses confirmed the presence of a geographic break at the equator separating the EPR fauna into two biogeographic entities, with one major split near the equator, somewhere between 9°50' N and 4° S. A secondary split, being more precisely located around 15° S, separates the SEPR into two smaller entities. However, species lists and molecular data between 9°50' N and 7°25' S are lacking, and further studies centred on the Hess Deep are needed to locate the break exactly. The two evolutionary lineages of *L. elevatus* were found in sympatry at 9°50' N and are able to hybridize (Matabos *et al.*, 2008a). Other cryptic complex species may also overlap around the equator. This is especially the case for *L. ovalis*, which showed a consistent but weak divergence between two distinct mitochondrial lineages that overlap along the SEPR. In contrast, the gastropod *E. vitrea*, which displays

the same level of divergence, exhibits a complete geographic separation of its two cryptic lineages at 7°25' S in a similar way to the polychaete *A. pompejana* (Plouviez *et al.*, 2009). One explanation could be the differences in life history strategies, which can influence dispersal abilities. Some species may indeed have the dispersal potential to cross the barrier and meet secondarily. Genome homogenization between the previously isolated clades then depends on the strength of the selection against hybrids (genetic barrier: Barton & Hewitt, 1985).

Added to the occurrence of cryptic species in the two parts of the EPR, the BIOSPEEDO cruise brought at least 10 new species for hydrothermal vents (three gastropods, seven polychaetes) and expanded the range of several species previously described from the NEPR. The wide geographic range of most vent species confirmed findings from studies previously conducted by Van Dover (2002) in the same area. However, while the first studies based on megafauna observations (Geistdoerfer *et al.*, 1995; Halanich *et al.*, 1999) and the quantitative analysis of communities associated with mussel beds (Van Dover, 2002, 2003) concluded that the fauna was similar between the northern and southern EPR, results from the present study highlight several latitudinal changes in community composition between 17° S and 21° S. New species were found beyond 17° S, and some species warrant further study as their identification remains uncertain (Hourdez & Desbruyères; A. Warén, pers. obs.). In the listed taxa, two species, *Shinkailepas* sp. and *Eosipho auzendi*, represented by two and more individuals, respectively, belong to genera so far known only from other ridge systems (Desbruyères *et al.*, 2006b), although the presence of *Eosipho* was previously reported at Rehu Marka by Van Dover (2002). Seen in conjunction with the presence of at least five cryptic species (i.e. *L. elevatus*, *L. pustulosus*, *L. tevianus*, *Peltoispira operculata*, *Pachydermia laevis*), it is apparent that the EPR is a more complex biogeographic zone than was first suggested. When taking into account only the species recorded in Desbruyères *et al.* (2006b), a geographic break was found at 18° S (Fig. 3a), and, while taxonomic diversity was higher at 17°25' S, the highest species richness was found at 13° N (Table 3). When combining species collected on the SEPR during the BIOSPEEDO cruise, both species richness and taxonomic diversity were no longer different between the NEPR and SEPR vent sites, and the geographic break along the SEPR appeared between 14° S and 17°25' S. The hypothesis of Bachraty *et al.* (2009) that the NEPR could be a centre of dispersal is probably a result of over-sampling in the northern part of the EPR. Indeed, the uneven sampling effort across hydrothermal vent ecosystems since their discovery, resulting from the poor accessibility of the vent environment, may well have generated biases in the data that led to incorrect biogeographic patterns. This may still be the case for underexplored regions such as the Pacific Antarctic Ridge and the Indian Ridge. We can, however, expect that the biodiversity of macrofauna is now well estimated for the most heavily prospected regions,

namely the NEPR, the Western Pacific back-arc basins and the Azorean plateau of the MAR.

Observations and molecular data led to the assumption that the high species diversity observed in the southern part of the SEPR is the result of the overlap of several distinct biogeographic provinces. The new species of *Phymorhynchus* sp. had already been found on the Pacific Antarctic Ridge (PAR) at 31° S (A. Warén, pers. obs.), in concordance with the presence of the gastropod *Eosipho auzendi*, described from the PAR. Individuals of *Shinkailepas* sp., a genus described only on the MAR and in the back-arc basins, were encountered at 21°33' S. Furthermore, the values for the average taxonomic distinctness for the sampling units collected in mussel beds located between 17°25' S and 21°33' S (i.e. Oasis BS6, Rehu Marka, Animal Farm and Grommit) are above the upper limit of the 95% confidence interval of the simulated values, reinforcing the hypothesis of an abnormal hotspot of diversity in this area. Similarly, the observed species richness values differ significantly from the predicted richness under the mid-domain effect null model, which predicts expected species richness values by considering the geometric constraints on the geography (Colwell & Lees, 2000). These results suggest that the southern part of the SEPR (i.e. between 17°25' S and 21°33' S) probably forms a transition (mixing) zone between the NEPR, the Pacific Antarctic Ridge, and, possibly, the back-arc basins of the western Pacific. This assumption is supported by the co-occurrence of NEPR-like *Alvinella* colonies and *Chorocaris* sp. swarms at 21°33' S, these shrimp swarms being one of the most striking characteristics of the MAR, the Indian Ocean Ridge and the western Pacific back-arc basins (Van Dover *et al.*, 2001; Jollivet *et al.*, 2005). The latitudinal gradient in species diversity reveals the influence of tectonic plates and ridge history but accounts for only 45.4% of the total variation of the species presence-absence in vent assemblages, highlighting the need to combine historical and ecological biogeography for a better understanding of current biodiversity patterns.

Biodiversity patterns at a regional scale: mussel beds along the SEPR

Species diversity associated with mussel beds was analysed along the SEPR in order to gain a better understanding of regional processes influencing community structure along the ridge. Diversity associated with mussel beds has been studied extensively along the EPR, for example by Turnipseed *et al.* (2003), Van Dover (2003), Bergquist *et al.* (2005) and Dreyer *et al.* (2005). Most of these studies were conducted using quantitative sampling that includes vagile epifauna and large macrofauna juveniles (e.g. crabs). This difference in sampling design can account for the lower species richness observed in this study compared with previous studies conducted along the SEPR (Van Dover, 2002, 2003). Results from the canonical analysis showed that latitude combined with the venting state at the regional scale is significantly correlated with the community structure and composition associated with mussel

beds along the SEPR. The sites Oasis (17°25' S), Rehu Marka (17°25' S), Animal Farm (18°36' S) and Grommit (21°33' S) were characterized by high diversity compared with the northernmost sites.

While the influence of the geodynamic environment was not significant, the analysis did show that the venting stage had a significant influence when combined with latitude. This result reflects the intermingling roles of local and regional factors. The type of venting is strongly related to the regional dynamics of the ridge (Fouquet *et al.*, 1994). All chimneys were found in vent fields characterized by a tectonic environment (i.e. Grommit, 21°33' S; and Susie, 17°34' S). Areas driven by volcanic activity are less stable in time and space than tectonic areas (Fouquet *et al.*, 1994). The instability caused by controlling the extinction rate of sites will impact the extinction/recolonization rate of the vent fauna, promote habitat heterogeneity and reduce distances between sites (Jollivet *et al.*, 1999). While unstable environments are expected to reduce species diversity by maintaining communities in a pioneer stage (Juniper & Tunnicliffe, 1997), it has been suggested that the resulting small distances between vent sites should account for bursts of gene flow (Jollivet *et al.*, 1999) and thus for a greater rate of site recolonization, promoting higher species diversity (Turnipseed *et al.*, 2003; Van Dover & Doerries, 2005). Furthermore, if taxonomic distinctness is expected to be a more sensitive univariate index to community perturbation than species diversity (Warwick & Clarke, 1995), species richness and taxonomic diversity were equivalent in the two types of vent dynamics, suggesting that differences resided mainly in species composition. As an example, three gastropod species (*Melanodrymia aurantiaca*, *Echinopelta fistulosa* and *Nodopelta subnoda*), known to colonize active black smoker chimney walls (Jollivet, 1996), were collected only at the Grommit site (21°33' S), where mussel beds developed at the base and on the wall of a black smoker. Similarly, scavenger species (i.e. *Phymorhynchus* spp., *Eosipho auzendi*, *Spioniphura jolliveti*) were found mainly in sites located in volcanic areas (i.e. Oasis BS6, Rehu Marka and Animal Farm).

On the other hand, while all sampling units collected from the tectonic 21°33' S vent field (Grommit) were similar in species composition, strong differences were observed between sampling units in the volcanic 17°25' S area (i.e. Oasis BS6 and Rehu Marka). In unstable volcanic areas, the high rate of spatio-temporal changes in fluid fluxes results in the intermingling of different successional stages within a site, thus enhancing the variance among mussel beds in a given area. For example, at the declining site Sarah's Spring, located on a dome-shaped ridge, the presence of small specimens of the tubeworms *Tevnia jerichonana* and *Oasisia* sp. (D. Jollivet, pers. obs.) suggests the (re)start of a new venting site at the immediate periphery of an earlier vestimentiferan community.

The major effect of venting state on mussel bed community arises from the decline in hydrothermal activity (i.e. moribund state). Edifice life spans are highly variable within a single vent field as a result of stochastic events altering fluid discharge and

mineralization processes. Variations in fluid discharge intensity have a strong influence on physico-chemical variables and biotic interactions between species (Mullineaux *et al.*, 2003), which will, in turn, greatly impact the community structure and composition. Species composition is thus highly variable in time and space within a single site, and large differences are observed according to the successional stage of the community at the time of sampling (Jollivet, 1996; Sarrazin *et al.*, 1997; Shank *et al.*, 1998). On the EPR, productivity, species richness and abundances of invertebrates associated with mussel beds appeared to be lower at waning and older sites than at young and active sites (Van Dover, 2003; Dreyer *et al.*, 2005). In this study, the age of mussel beds was unknown, and the temporal state of mussel beds was assessed via the demographic structure of mussel populations and the proportion of juveniles. No correlation has been found between community structure and the mussel size frequency distribution (unpublished data) or the proportion of juvenile mussels. This proportion was high at the declining site Animal Farm (i.e. 56%, Table 1), while a low proportion of juveniles characterized the large and dense mussel beds developing in the healthy site Grommit (21°33' S) (i.e. between 0 and 9%). Thus the proportion of juvenile mussels does not appear to be a good proxy for characterizing mussel bed conditions and does not reflect *in situ* observations of the vent community (e.g. the presence of decaying vestimentiferan tubes at Sarah's Spring). Nevertheless, the apparent declining site Sarah's Spring exhibited a low diversity, as expected from previous observations on mussel beds (Van Dover, 2003), with an overwhelming presence of the gastropod *L. elevatus* (48%) and the polychaete *Amphisamytha galapagensis* (37%). By contrast, the other declining site (i.e. Animal Farm), located on a dome-shaped ridge, is characterized by a high diversity.

Latitudinal gradient and venting stage explained less than half of the variation in the species data, suggesting that other local biotic (e.g. predation, competition) or abiotic (e.g. small-scale habitat heterogeneity) factors independent of the type of venting, as well as metacommunity neutral dynamics, may account for a large proportion of the observed variation. Manipulative field experiments showed that biological interactions, including facilitation and competition for space and/or food availability, could strongly modify the community structure in the absence of temporal changes in physico-chemical conditions (Micheli *et al.*, 2002; Mullineaux *et al.*, 2003). Similarly, recent studies have suggested that most hydrothermal gastropod species are not exclusive to a specific habitat type, as they may occupy specific microhabitats (Mills *et al.*, 2007; Matabos *et al.*, 2008b). However, despite the lack of replicate sampling units, the influence of local factors is not sufficient to totally blur the effects of regional and global factors related to the latitudinal gradient.

Limitations and issues

The recent discovery of cryptic species following the emergence of barcoding approaches and molecular taxonomy raises the

problem of species identification and thus the assessment of vent biodiversity (Vrijenhoek, 2009). This appears to be a general issue in the marine environment. Ubiquitous species are frequent among marine invertebrates and vertebrates, and are often found over a wide range of latitudes from the poles to the tropics (Knowlton, 1993). Good species identification is needed in order to understand vent community history, colonization pathways and the origin(s) of the fauna. These observations reinforce the importance of comparative phylogeography for complementing analytical approaches of historical biogeography (Arbogast & Kenagy, 2001). Correct assessments of species boundaries are fundamental to the testing of biogeographic hypotheses (Palumbi, 1996). Furthermore, species identifications are not always conducted by specialists, a fact that leads to difficulties in comparisons between taxa lists. Valid comparisons across studies require a standardized process for the identification of organisms. This raises another issue related to species recording and species distribution areas and the validity of lists available in the literature. Individuals identified by acknowledged specialists and recorded in a museum with a barcode and a voucher number appear to be a safe standard for biodiversity assessment and record. However, ecological studies are more numerous than taxonomic ones, and numerous species lists are provided by ecologists (Van Dover, 2002, 2003; Govenar *et al.*, 2005; Matabos *et al.*, 2008b), making it very difficult to assess the real biodiversity associated with each of the EPR segments. Differences in sampling method (i.e. quantitative versus qualitative) can also account for the differences observed. Sampling devices have been independently developed in different laboratories and may thus not be comparable. Finally, the status of rare species should also be seriously considered in biogeographic approaches. Most ecological studies focus on a particular vent habitat, and, as a result, may underestimate the 'real' local biodiversity. To our knowledge, the sediment habitat surrounding vents has been severely neglected, so that many species may have never been collected.

This study not only reinforces the existence of two biogeographic provinces along the EPR, the northern and the southern EPR, but also suggests that the 'abnormal' high species diversity associated with the southern part of the SEPR (17° S–21° S) could result from the overlap of several biogeographic entities. Additional samples from the poorly explored Pacific Antarctic Ridge area could help us to gain an understanding of biodiversity patterns associated with the Pacific hydrothermal vent systems. Combining species diversity analyses with comparative phylogeography will help to unveil colonization pathways that have led to the present species distribution. On the other hand, the lack of standards in species classification for deep-sea biogeography and of cross-validation of species identification could explain the discrepancies observed when comparing studies conducted in the same parts of the ocean. The analysis of diversity associated with mussel beds is a first step towards a better understanding of the effects of global, regional and local factors on

biodiversity patterns. In this study, a combination of the latitudinal gradient and the venting stage significantly influenced the community structure, but more replicates and explanatory variables are needed to ascertain such a finding. This study will help in the design of future macroecology studies along the EPR that aim to understand processes influencing the distribution of biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species list of macrobenthic invertebrates along the East Pacific Rise (EPR).

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BIOSKETCH

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